THE PHRYMACEAE IN THE SOUTHEASTERN UNITED STATES 1

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PHRYMACEAE Schauer in A. P. de Candolle, Prodr. 11: 520. 1847.

(LOPSEED FAMILY)

A monotypic family ² of herbaceous dicotyledons distinguished by perfect, hypogynous, zygomorphic flowers; synsepalous calyx with the 3 upper lobes subulate and hooked; sympetalous 2-lipped corolla; 4 epipetalous stamens; pseudomonomerous gynoecium with a basal orthotropous to hemianatropous ovule; and an achene enclosed in the accrescent calyx. Type genus: *Phryma* L.

The Phrymaceae are of somewhat uncertain taxonomic status. They are regarded as allied most closely to the Verbenaceae, differing principally in the solitary ovule and the superior radicle. In stem anatomy, *Phryma* is similar to "certain members" of the Verbenaceae (Smith). According to Lipscomb, in general vegetative form, inflorescence type, and flower and fruit anatomy *Phryma* has its closest affinities with the tribe Lantaneae of the Verbenaceae and is structurally most similar to the genus *Stachytarpheta*; she favors tribal status for *Phryma* in the Verbenaceae. Other authors (Baillon; Bentham & Hooker; Hutchinson, 1926) have included *Phryma* among the Verbenaceae, but it is more commonly treated as the sole genus of a distinct family.

The Phrymaceae, along with the Globulariaceae and Littorella and

¹Prepared for a generic flora of the southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium of Harvard University made possible through the support of the National Science Foundation (Grant GB-6459X, principal investigator Carroll E. Wood, Jr.). This treatment follows the format established in the first paper in the series (Jour. Arnold Arb. 39: 296-346. 1958). The area covered includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. References that I have not seen are marked with an asterisk.

I am indebted to Dr. Wood for his careful review of the manuscript and for other aid; to Ralph Andrews and Fran Uhler for data on wildlife use of *Phryma*; and to the curators of herbaria who responded to my request for distributional data on *Phryma*. The illustration was made by Rachel A. Wheeler from dissections by Dr. Wood.

² Melananthus Walpers was originally described as a second genus of the Phrymaceae. Its systematic position was considered doubtful by Bentham & Hooker. Later, Taubert reaffirmed the affinity between it and Phryma. Finally, on anatomical and morphological grounds, Solereder transferred the genus to the Solanaceae, tribe Salpiglossideae.

Bougueria of the Plantaginaceae, provide good examples of pseudomonomerous gynoecia (Eckhardt, Wilson & Just). Such a gynoecium, actually a syncarpous structure, has the appearance of a single carpel; it develops through suppression of all but one of the original carpels. In *Phryma*, the gynoecium is viewed as being two-carpellate, with one carpel (the posterior?) being reduced. Lipscomb found the gynoecium to be "bicarpellate as indicated by two dorsal bundles which extend the length of the pistil."

1. Phryma Linnaeus, Sp. Pl. 2: 601. 1753; Gen. Pl. ed. 5. 262. 1754.

Simple or branched perennial herbs. Leaves opposite, simple, serrate to crenate-serrate, the lower long-petioled, the upper nearly sessile. Inflorescences of terminal, long-peduncled, spikelike racemes. Flowers perfect, zygomorphic, hypogynous, axillary to bracts, horizontal at anthesis,

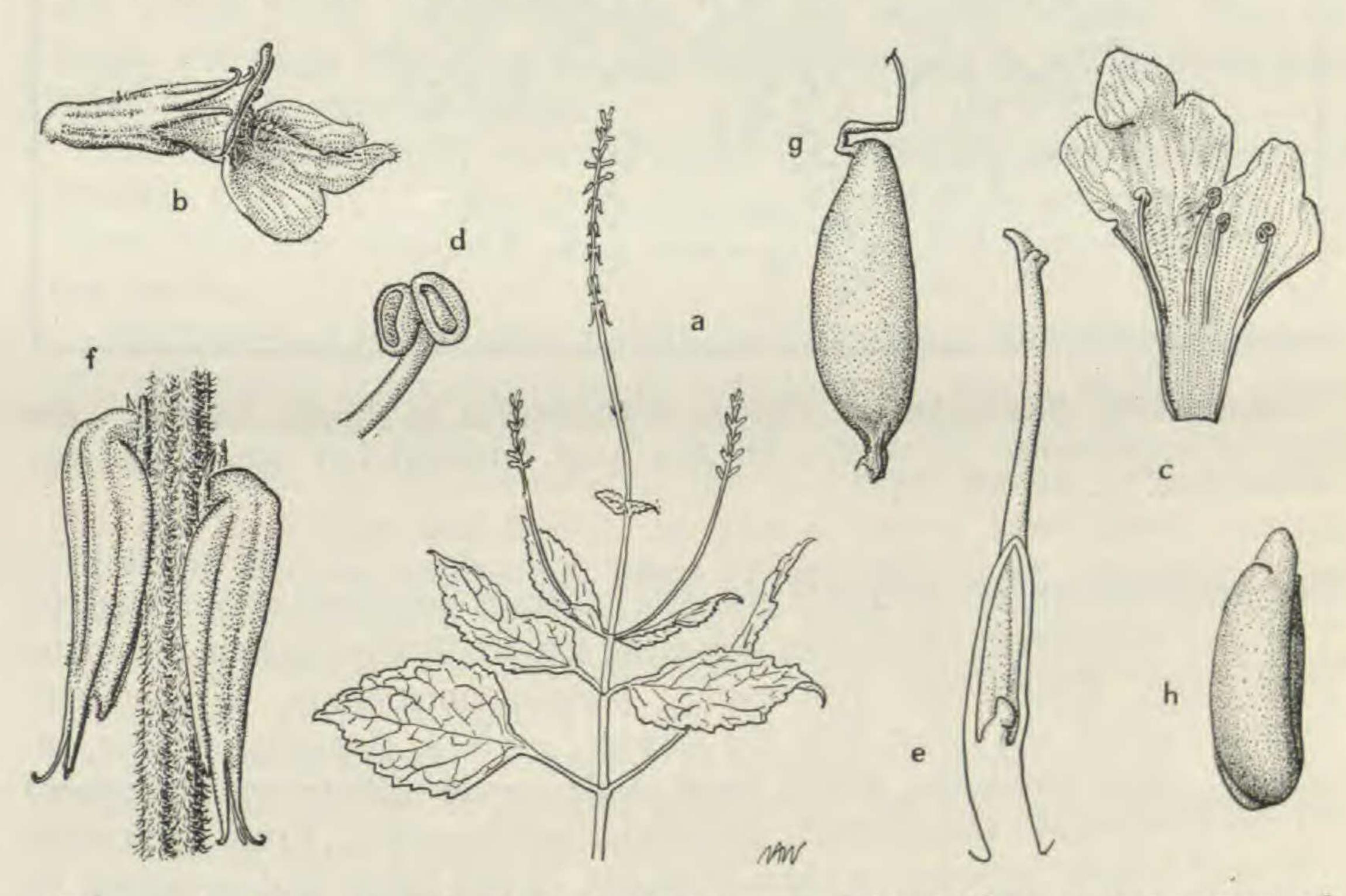
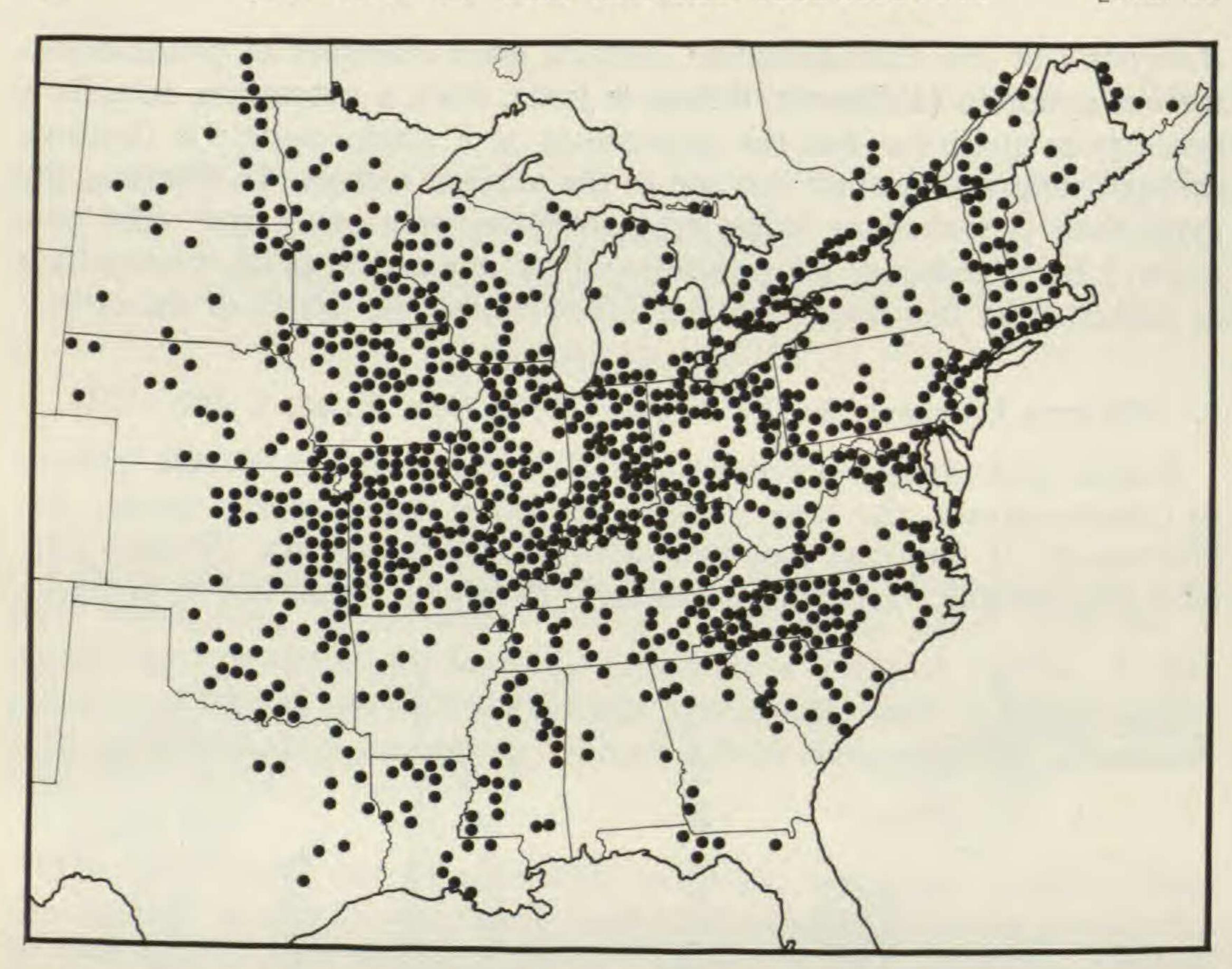


FIGURE 1. Phryma. a-h, P. leptostachya var. leptostachya: a, upper part of small plant with flowers and young fruit, \times 3/8; b, flower, \times 4; c, corolla laid open, \times 4; d, anther, \times 20; e, gynoecium in vertical section to show ovule, \times 15; f, nearly mature fruiting calyces, \times 4; g, fruit, \times 5; h, embryo, \times 5.

sharply reflexed soon thereafter, opposite or sometimes the lower ones alternate, the pedicels short, bibracteolate. Calyx persistent, synsepalous, cylindrical, strongly zygomorphic, 2-lipped, the upper lip of 3 subulate, hooked lobes about equalling the tube at anthesis, the lower much shorter, of 2 triangular lobes, the tube sulcate, accrescent in fruit. Corolla sympetalous, the tube cylindrical, the limb 2-lipped, the upper lip upwardly diverging, notched, external in the bud, the lower lip much longer, horizontally projecting, 3-lobed, the palate uparching, 2-ridged centrally. Androecium didynamous, the stamens included, alternate, epipetalous, the



Documented distribution of *Phryma leptostachya* in North America. For map of approximate distribution in Asia (var. oblongifolia) see Trans. Am. Philos. Soc. II. 42: 422. 1952.

lower pair the longer; filaments elongate; anthers dorsifixed, 4-sporangiate, 2-locular at anthesis, the locules dehiscing longitudinally; pollen 3-colpate, subprolate. Gynoecium syncarpous, pseudomonomerous, 2-carpellate; stigma 2-lobed, the upper lobe the shorter; style 1, elongate, slender, included; ovary unilocular, with 1 basal ovule; ovule orthotropous (Cooper) to hemianatropous (Lipscomb), unitegmic, tenuinucellar. Fruit a narrowly ellipsoid achene included in the accrescent, closed calyx that is tipped by the 3 indurated, hooked, upper lobes; seed filling the fruit, endosperm thin (2 cell layers), the embryo with convolute cotyledons. Embryo sac development normal (Polygonum type); radicle superior; endosperm ab initio cellular, with a 4-celled chalazal haustorium. Type species: P. leptostachya L. (Derivation of the name unknown.³) — Lopseed.

A genus of a single species with bicentric distribution in mesic to moist, deciduous or mixed forests of eastern North America and southeastern Asia. Phryma leptostachya L. ranges in the New World, as var. leptostachya, 2n = 28, from New Brunswick to Wisconsin, extreme southwestern Ontario, and southwestern Manitoba south to western Nebraska, eastern Texas, and northern Florida, and as var. confertifolia Fern. (of

³ Kuprianova asserts that Phryma is a native Amerindian name.

dubious taxonomic significance), from eastern Virginia to Delaware; 4 and in Asia, as var. oblongifolia (Koidz.) Honda (var. asiatica Hara, P. asiatica (Hara) Degener & Degener), $2n = 28,^5$ from the Himalayas to Manchuria, southeasternmost Soviet Union (Primorski Krai), Japan, and North Vietnam (Tonkin). The Asiatic plants differ only slightly from the American ones, mainly in pubescence, length of the upper calyx lobes, shape of the upper corolla lip, and often smaller corollas (Hara).

The flowers open at various times during the day or night, but usually in the morning. In bud they are ascending, but as anthesis approaches they gradually become horizontal. Usually both flowers of a pair open more or less at the same time, but occasionally one may open as much as 36 hours after its mate. Anthesis typically proceeds regularly up the raceme, although sometimes a pair may open a full day before the pair below it. Individual flowers last 12–36 hours, after which the corolla drops, and within 24–48 hours the flower becomes sharply reflexed. After anthesis, the calyx tube (but not the lobes) increases in size and the three upper lobes become indurated.

The corolla is white, with the upper lip and sometimes the lower one strongly pink tinged. The calyx tube and lower lobes are green, but the upper lobes are either the same shade as or a pink darker than that of the corolla.

The flowers of *Phryma* are strongly proterandrous. According to Robertson, pollination is accomplished by long-tongued insects, including *Halictus purus* (*Augochlora pura*), a mining bee; short-tongued insects are excluded from the corolla tube by the up-arching palate, although small bees can force their way into it. In spite of several hours spent watching plants of *Phryma* at various times of day and night (on South Bass Island, Ottawa County, Ohio) the author never saw an insect visiting one.

The disseminules are the indehiscent fruits enclosed in the accrescent calyx tube. Three of the calyx lobes are much longer than the other two and are hooked apically. Dispersal is presumably epizoöchorous (Ridley). Dispersal in the fur of animals apparently has not been demonstrated, but hooking onto clothing can take place.

An extract of the leaves and roots of *Phryma* has been found to possess insecticidal properties. The active principle, phrymarol, is evidently a "kind of sterine" (Kikutani & Oshima). In the lower Yangtze Valley, the Chinese name of *P. leptostachya* means "poisonous fly-plant" (Steward), and in Japan the plant "is used to kill the common houseflies" (Matsuzawa).

The fruits of Phryma are known to be eaten by wild turkeys in Virginia.

^{*}Phryma was collected about a century ago in Bermuda, but "probably only as a waif" (Britton).

Darlington & Wylie's assertion (Chromosome atlas of flowering plants, p. 323. 1955) that Sugiura (Cytologia 7: 587. 1936) reported a diploid number of 14 for *P. leptostachya* is erroneous; he reported a *haploid* number of 14. This same error is repeated by Bolkovskikh, Grif, Matvejeva, & Zakharyeva (Chromosome numbers of flowering plants, p. 486. 1969).

Among the fungi that parasitize *Phryma* are two, *Puccinia extensicola* var. *phrymae* (*Aecidium phrymae*) and *Septoria leptostachya*, the names of which commemorate their host.

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